

Pollen Dispersal by Catapult: Experiments of Lyman J. Briggs on the Flower of Mountain Laurel

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The flower of *Kalmia latifolia* L. employs a catapult mechanism that flings its pollen to considerable distances. Physicist Lyman J. Briggs investigated this phenomenon in the 1950s after retiring as longtime director of the National Bureau of Standards, attempting to explain how hydromechanical effects inside the flower's stamen could make it possible. Briggs's unfinished manuscript implies that liquid under negative pressure generates stress, which, superimposed on the stress generated from the flower's growth habit, results in force adequate to propel the pollen as observed. With new data and biophysical understanding to supplement Briggs's experimental results and research notes, we show that his postulated negative-pressure mechanism did not play the exclusive and crucial role that he credited to it, though his revisited investigation sheds light on various related processes. Important issues concerning the development and reproductive function of *Kalmia* flowers remain unresolved, highlighting the need for further biophysical advances.

Key words: Biomechanics; biophysics; Lyman J. Briggs; *Kalmia latifolia*; elastic properties; catapult; negative pressure; pollen dispersal; botany; plant-water relations.

Introduction

Some biomechanical processes depart so far from our ordinary observations of physical phenomena that their workings are mysterious to experts; like an unexplained magician's trick, they appear to violate natural laws. The mechanism by which *Kalmia latifolia* abruptly flings its pollen into the air in response to the

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proximity of pollen-carrying insects is one such case. This phenomenon captured the attention of the noted American physicist Lyman J. Briggs (1874–1963) after he retired from his 1932–1945 tenure as director of the National Bureau of Standards (NBS),* the United States' ultimate authority on physical measurements. Over several years in the 1950s, Briggs conducted experiments on *Kalmia* flowers and tested hypothetical explanations, leaving handwritten notes and an unfinished manuscript now filed at the (US) National Archives. Our interest in the subject of pollen discharge by *Kalmia* stemmed from an earlier, broad look at Briggs's life and scientific career.¹ In this paper, we report our analysis of Briggs's investigation and results of our own follow-up experiments aimed at explaining how *Kalmia* disperses its pollen. The topic affords an interesting exploration of the physics of interacting bulk fluids and solids in a biological system.

Rapid movements in plants have been a subject of continuing botanical and physical interest. Recent scientific investigations have focused on the hydraulics and mechanics of such movements.² King and Buchman investigated the importance to pollen dispersal of vibrational resonances in *Rhododendron* stamens.³ Flowers of the genus *Kalmia* (figure 1) display a catapult release of pollen that has long attracted attention.** Noted American botanist William J. Beal, a student of Asa Gray at Harvard, described the release of pollen by *Kalmia* as follows:

When the anthers are liberated from the pockets in the corolla, the stamens suddenly straighten and throw jets of pollen often a foot or more, "acting," as Professor Gray used to say, "like a boy's pea-shooter."⁴

Investigations like these are important as case studies of sudden, rapid, macroscopic motion of plant tissues, a response employed by many species for specific functions, and of the interactions among plant structural elements, internal fluid state, and environmental influences in determining biological function.

Pollen Distribution and Rapid Motion of Flowering Plants

Plants have no muscles to propel movement. Those that need substantial movement, for example for a flower to face the sun as it moves in the sky, must do so through mechanical action of tissues and cells. Most such movements are slow, acting over a few hours. Some are faster; for example, the stamens and stigmal lobes of some flowers bend in a matter of seconds when touched by insects.⁵ But fraction-of-a-second movements of flower parts are rare and are sometimes associated with pollen release by an explosive or catapult means.⁶

* After 1988, the National Institute of Standards and Technology (NIST).

** Figure 2 defines "corolla," "stamen," and other botanical terms. An anther is the end portion of the stamen, which contains the pollen. Stamens, each of which is the active member of a catapult, are visible in figure 1 as curved filaments about 10 mm in length with their basal ends attached to the center of the flower.



Fig. 1. Flower of *Kalmia latifolia*. The 10 pockets in which the upper portions of the anthers are lodged are located approximately midway between the base and the free edge of the corolla. The paperclip is 2.5 cm long. Credit: E. R. Landa.

Kalmia is a North American genus of shrubs within the heath family (Ericaceae) that occurs from Alaska to Cuba. It is classified within the large subfamily Ericoideae, along with diverse genera including *Rhododendron* and *Erica*.⁷ The most familiar of the seven or eight recognized species within the genus is *Kalmia latifolia*, commonly known as mountain laurel and widely distributed in eastern North America. Because of its beauty, mountain laurel was proposed as the national flower of the United States; it is the state flower of Connecticut and Pennsylvania.⁸

The small flowers with five petals (about 20 mm diameter when open) occur in clusters. The distinctive, pollen-discharge mechanism of the ten stamens in *Kalmia* (figures 1 and 3) has been described by Ebinger:

Near the middle of the corolla are 10 pockets forming small lobes on each ridge of the flower bud. ... Just before the bud opens, the elongating filaments push the anther upward into these pockets. As the corolla opens, the elastic filaments bend backward under tension, and the anthers are held in the pockets and carried down and outward. When the flower is disturbed by a large insect, one or more of the anthers is released. When this occurs, the tension of the elastic filament is strong enough to throw the pollen [7.5–15 cm] from the flower.⁹

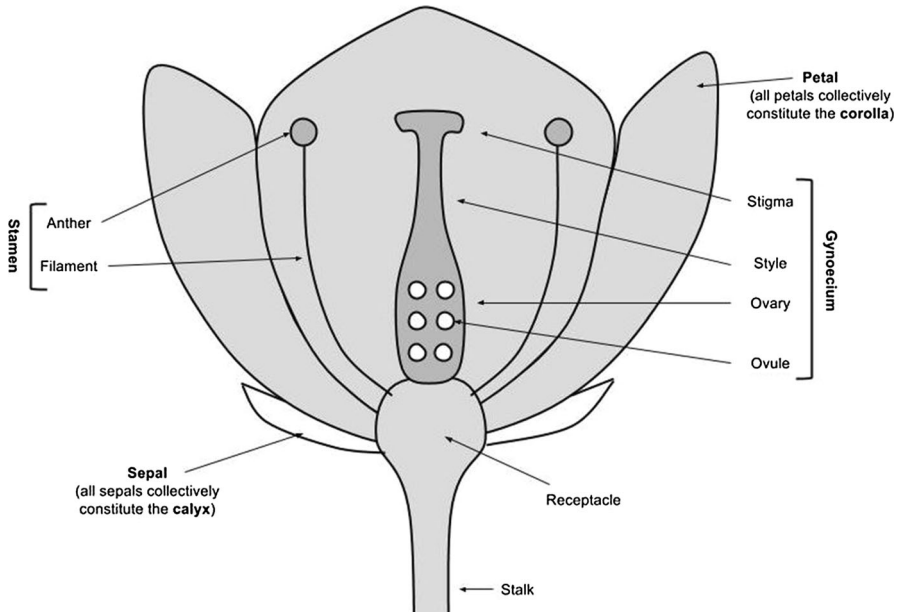


Fig. 2. Diagram of an idealized flower, with major components labeled.

Developing in the bud, the filaments, which initially curve slightly inward, start to turn outward and then upward (figure 3a) so that the upper end of each anther fits into one of the corolla pockets (figure 3b), a position achieved before the flower opens. When the flower does open, the anthers remain in the pockets of the saucer-shaped corolla and the filaments assume a flattened, elongated S-shape, except at the top. Mechanically, the stamen acts as a cantilever spring, fixed at the basal end, with the stamens bent away from what would be their free or unstressed shape, as can be seen in figure 1. Before flinging, with the distal end in the corolla pocket, a restraining force exerts bending stress.¹⁰ Stiffness of the corolla, essential to generate this force, is characteristic of *Kalmia* flowers. The corolla can be described as a distinct firm bowl; it is commonly observed intact on the ground in mountain laurel groves after the blooming period. When the anther is yanked out of its pocket by an insect accidentally tugging on the filament, the stress already established within the filament makes it rapidly bend away from the petal toward the center of the flower, immediately flinging the pollen, some of which may land on the pollinator's body or the stigma. Some observers have reported that the stamen can be spontaneously released towards the end of floral life, while others have noted that when the flowers are protected by netting to exclude insects, none of the stamens are released (the anthers remain in the pockets and the filaments lose their elasticity) and no seed is produced.¹¹

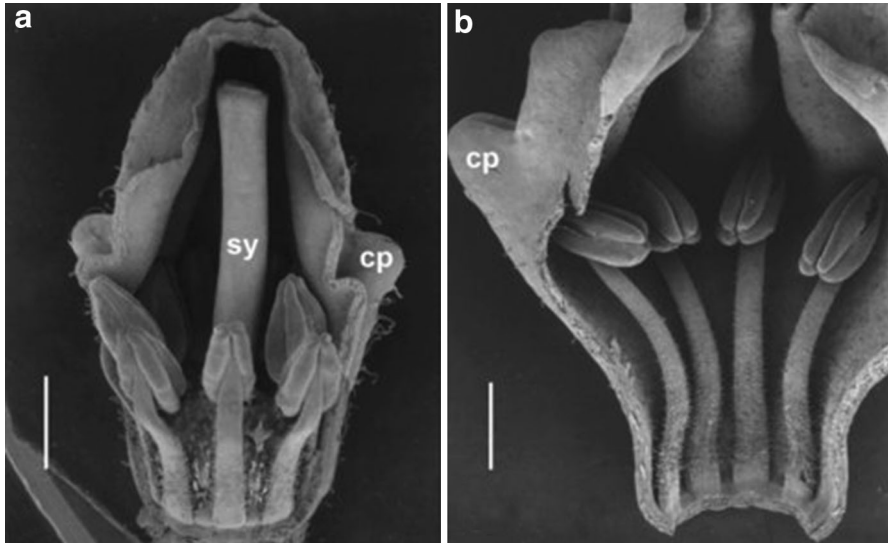


Fig. 3. Buds of *Kalmia latifolia*. (a) Young bud showing early corolla pockets with stamens still essentially upright. (b) Older bud showing stamens bending toward the corolla pockets. Scale bars = 1 mm. *Figure abbreviations:* cp, corolla pocket; sy, style. Source: Hermann and Palser (ref. 29), with permission from *American Journal of Botany*.

Briggs and his *Kalmia* Investigation

Briggs's career began with his employment at the US Department of Agriculture (USDA) in 1896.¹² At age twenty-three, he published an explanation of the roles of surface tension and gravity in determining the state of static soil moisture.¹³ These concepts likely helped to underpin the work of his junior colleague Edgar Buckingham, who in 1907 introduced the concept of matric potential (the component of energy that arises from the water's interaction with the rigid soil matrix) in soil-water flow.¹⁴ Around this same time, Briggs and coworkers developed the soil moisture-equivalent concept, whose measurement involving negative (less than atmospheric) pressure produced by outflow of water from a sample in centrifuge. In the next decade, Briggs's multi-state experiments with H. L. Shantz on water use efficiencies showed that in a climate like that of the Great Plains, plants use water more productively in the cooler north than in the warmer south. These experiments have resonance today in the economics of agricultural production in various climate regions of the United States and elsewhere.

During World War I, Briggs transferred to the NBS to work on defense-related topics. These investigations included the design and construction of a wind tunnel with air speeds approaching the speed of sound for research on improved designs for propellers. His work for the US Navy included the development of a "stable zenith" device, a gyroscopic instrument for maintaining an artificial horizon to aid

large guns on naval vessels to direct their fire. The device designed by Briggs and coworkers was tested aboard the battleships *USS Arizona* and *USS Mississippi* in October 1918 and later was deployed to the entire battleship fleet.

Following World War I, Briggs continued his research and administrative duties at NBS, rising to its directorship in 1933. Among his contributions to the American scientific community was his leadership, beginning in 1939, of a top-secret committee that evolved into the Manhattan Project to develop an atomic bomb. Briggs retired as NBS director in 1945 and returned to laboratory studies. A life-long baseball fan, at age eighty-four Briggs studied the speed, spin, and deflection of the curve ball, aided by manager Cookie Lavagetto and the pitching staff of the Washington Senators; he published these findings in the *American Journal of Physics*.¹⁵

Briggs's major thrust after 1945, however, was a return to the subject of negative pressures. The central issue he explored was how great a magnitude of negative pressure a liquid can sustain. The basic method of these studies was to apply force that tends to pull apart a continuum of liquid in a tube, increasing the force to decrease pressure within the liquid. When intermolecular forces are sufficiently exceeded somewhere, cavitation occurs: a bubble of vapor is created that immediately expands and breaks the continuity of the liquid mass. Briggs used a centrifuge with an open-ended tube of liquid, horizontal in the plane of rotation and centered on the axis of rotation. Centrifugal force would pull liquid outward toward both ends, creating a calculable negative pressure at the center. Briggs found that, with adequate attention to experimental details and cleanliness, the liquid could sustain extreme negative pressures without cavitation. For liquid water, he established negative pressures as great as 277 atmospheres. Between 1949 and 1957, Briggs published eight sole-author journal articles on negative pressure in *Science*, the *Journal of Applied Physics*, and the *Journal of Chemical Physics*. This work is still cited in the modern plant physiology literature on the ascent of water in xylem (a plant tissue) as supportive of the cohesion theory; proponents of the theory use the high tensile strength of water found by Briggs to explain how water can reach the top of tall trees.¹⁶

The curious circumstance of a soil physicist assuming a leadership role in the Manhattan Project initially attracted our attention to Briggs more than a decade ago.¹² The latter role was associated with his position as the highest-ranking physical scientist in the federal government, giving him a status akin to the present-day presidential science advisor. In speaking with people over the years about Briggs, it has been interesting to find that each science community knows Briggs for a different reason, and each is typically unaware of his other work—the aerodynamics community knows his wind tunnel work, but the soils community knows his moisture retention studies. His role in the science-of-baseball community is, of course, one that crosses many boundaries. The day in 1958 that Briggs came to Griffith Stadium is well remembered by Washington Senators pitcher Russ Kemmerer:

I was with the Senators at that time and I do remember all the fuss around the clubhouse because there were men attempting a science project that would prove what most baseball players took for granted, the thrown baseball does curve. Camilo Pascual had the best curve ball on the Senators, in fact it was the best in the American League, perhaps all of baseball. [Pedro] Ramos, on the other hand, had trouble making it bend. Lavagetto choose the two Cubans for the experiment. As a result the rest of the pitching staff became playful participants sticking in our two-bits whenever possible. I am not certain, but since the Senators were at home and since Ramos and Pascual did take part my participation in the event may have been limited simply because as a starting pitcher I was most likely scheduled to pitch that day or the next and Cookie would not have had us throw prior to our regular rotation.¹⁷

After Briggs's six decades of working with the precise physical character of hydraulic and mechanical processes, it is not surprising that he would be fascinated by the mechanism causing the mysteriously rapid and sudden motion of the *Kalmia* stamen dispersing pollen. He likely observed a prominent stand of *Kalmia latifolia* in Rock Creek Park in Washington, DC, near his home and workplace. The pollen-flinging process could easily be seen as less akin to the typical dynamics of plants than to those of human-engineered mechanical devices like catapults. One can see how this comparability might well have resonated with Briggs's long experience exploring technological devices, including many employing projectiles or explosives, for example the naval guns of World War I and nuclear bombs during World War II. The observation of similar dynamics in the living tissues of a flower would naturally inspire him to investigate this process.

Because Briggs was the former director of a federal agency, after his death his papers were transferred to the (US) National Archives and Records Administration (NARA). These materials include a loose-leaf binder labeled "negative pressure as an active agent in throwing pollen by Mountain Laurel (*Kalmia latifolia*).” The material therein covers the period 1954–1958 and includes laboratory notes by Briggs, notes to Briggs by Dr. J. M. Frankland, a specialist in solid mechanics at NBS, and ten handwritten pages by Briggs of a May 1958 manuscript draft.¹⁸ These archival materials inform us concerning what Briggs did and hypothesized about this phenomenon.¹⁹

Briggs directly explored the mechanisms responsible for the surprisingly sudden and forceful ejection of pollen from the *Kalmia* flower. Elements required for a catapult mechanism include a beam capable of maintaining a strong bending stress, a device for holding that beam in a stressed position, and a means of abrupt release so the stress can generate a rapid flinging motion. In the *Kalmia* flower, the stamen's thin filament is the beam, the pockets in the corolla hold it bent, and an insect in motion triggers the release. But other answers are not obvious, including (1) what processes act to generate the bending stress and (2) what properties of the filament allow it to achieve and maintain the required stress. In a mousetrap, by

analogy, the bending stress is created by forcibly bending the wire hammer from its original position to its set position. Properties needed by a filament, mousetrap, or other catapult-like device include stiffness adequate to establish substantial stress with a single bend through a given arc, elastic limit great enough to maintain the bend without losing the stress through deformation, and strength sufficient to withstand the bending stress without rupture. Briggs's work relates to these unsolved issues, with emphasis on the properties of the filament.

Given that Briggs was a world expert with sixty years of experience on the behavior of liquids under negative pressure, it is also not surprising that he hypothesized a major role for negative pressure within the filament's tissue in generating and maintaining the required stress. Briggs had formulated a hypothesis, unfortunately not explicitly stated in his notes, that some volume of liquid at negative pressure within the filament was essential to the mechanical process of triggered, rapid-motion flinging. The earliest indication of such a hypothesis appears in Briggs's lab notes of June 1, 1954. Briggs headed the page: "Differential negative pressures in the stamens of *Kalmia latifolia*." He had apparently already begun experiments, noting that attempts to release a single stamen and measure the stress on it were proving very difficult due to the twisting of stamens. From his notes and unfinished manuscript, we infer that his main objective was to establish that mechanisms not involving negative pressure were inadequate to generate and maintain the required bending stress.

A compressive stress generated by negative pressure in a longitudinal liquid-filled chamber inside the filament could alter its elastic properties, perhaps allowing it to bend further or spring back with greater force.* Such alterations of the tissue's properties may be necessary to accommodate the unusually high stress and strain required. Another hypothesis is that an internal negative pressure could generate a bending stress if the filament is asymmetric in the right way; a stress tending to curve the filament adaxially (opposite to its pre-flung curvature) could be generated by negative pressure if material of the adaxial side is thinner or softer. (The terms adaxial, meaning toward the flower's axis, and abaxial, meaning away from the axis, occur frequently in describing the characteristics and motion of the stamen.)

Briggs's notes describe an indirect, two-stage approach. First he measured stress and strain in the active filament. He undertook to measure the force exerted by a bent, stressed filament that had not yet flung and estimate its bending moment, the product of the transverse force applied by the petal to the bent stamen and the distance of the stamen's anchored base to its pinned anther. The bending moment is a measure of the internal stress induced by a given force applied at a given distance from the point where the filament is held fixed. Then

* Quantitatively, these properties are represented by the elastic limit, which indicates how much bending can be sustained without damaging the ability to spring back, and Young's modulus, the amount of bending force associated with a given degree of bend.

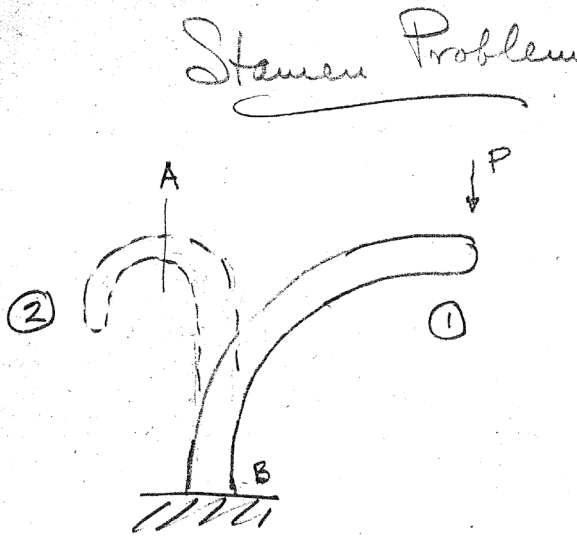


Fig. 4. Sketch by J. M. Frankland showing the initial and final positions of the *Kalmia* stamen associated with its triggering and subsequent pollen release. Source: ref. 19.

Briggs explored the possibility that these values, which allow the filament of the *Kalmia* stamen to spring forcefully enough to drive pollen out of the anther, could reside in the filament's material in the absence of negative pressure in the internal liquid. In Briggs's words, he was testing "the assumption that the pronounced elastic property of the filament arises from stretched fibers." If the required stress and strain were incompatible with the elastic properties of the filament material, then something else was required, quite likely a hydromechanical role of internal fluid pressure.

Briggs performed experiments on open flowers, freshly collected on the NBS campus in northwest Washington, DC, to determine the dimensions and mechanical stresses of the stamens. The small size of the flower (stamens are about 5–10 mm long) made the measurements a challenge. Additionally, the time window each year for obtaining open flowers with pinned stamens was narrow, a few weeks in late May to early June at that location.

Figure 4, taken directly from the archived materials, diagrams two positions of a stamen's filament: (1) curving abaxially before flinging when it is pinned in its corolla pocket and (2) curving adaxially after flinging that has taken it through a 270° rotation. Thus, position (2) is the free shape of the filament when no external stresses act on it.

What Briggs measured is the force exerted by the corolla to keep the stamen bent into position 1. Early attempts involved the release of a single stamen from its

pocket and constraining its escape by a hook applied near its tip, but the filament always twisted away. Briggs settled on a method that involved cutting a small section of the corolla containing several stamens to separate it from the remainder of the corolla. In so doing, he carefully left the anthers in their pockets so that the cut section was suspended by the stamens in nearly its original position. The central component of the flower, the gynoecium (figure 2), was apparently removed at the start of the procedure, probably to accommodate the greater-than-90° arc sometimes seen by Briggs with the released stamen. The weight of the cut section was not sufficient to offset the bending stress exerted by the stamens, so that the corolla section would be lifted a short distance upward and inward towards the central axis of the flower. Early trials looked at cut sections bearing 6–10 pockets; eventually a section with 2 stamens was deemed optimal. Cutting the corolla section was a tricky procedure involving a specially improvised holder for the flower and the use of a hand rest, razor blades, and manicure scissors. Briggs's lab notes of May 26, 1958 (the last entry we have) describe making the final cut to release the section: "This is ticklish. Many casualties."

Prior to cutting the corolla free, a wire hook was attached to the corolla between and below two adjacent pockets. Sections of fine chain with known weight per unit length were attached to the hook (sections of the chain and the hook Briggs used are preserved at NARA). The initial load was selected, based on experience, to hold the section near the pre-release "equilibrium" position. The chain was attached to a mini-windlass of design similar to Chainomatic analytical balances common in laboratories of the 1950s.²⁰ Additional weighted chain was dispensed until the cut corolla section returned to its initial position in the intact corolla. The combined weight of the hook, chain, and fresh corolla section (the latter weighed at end of run) was used to calculate the upward force exerted by the still-attached stamens.

The force required to maintain a filament in the bent, stressed configuration it has when pinned, based on nine measurements, was 280 ± 30 micronewton, equivalent to about one-third the weight of a bee. The angular rotation of the tip of the filament in going from pinned to released position was as much as 270°.* Frankland used Briggs's data to calculate conditions and properties related to bending. For the bent stamen of *Kalmia*, he calculated the bending moment to be 2.0×10^{-6} newton meter, the bending stress 0.12 megapascal (best value), and the extreme fiber strain 0.047. Briggs interpreted these results with respect to plausible alternatives for the physical mechanisms responsible.

To estimate the maximum flexure possible without negative pressure augmentation, Briggs looked to measurements of other botanical materials. His line of

* Briggs measured the filament length to be 11 mm, the straight-line distance between the fixed and pinned ends of the bent filament 7 mm, the filament width 0.44 mm at midpoint and 0.56 mm near the basal end, and thickness (from abaxial to adaxial edge) 0.25 mm. The pinned filament was bent abaxially 90°; some time after flinging it was bent adaxially 180°.

reasoning was that if botanical materials in general were insufficiently elastic to sustain the flexure he had measured in the filament, then an additional influence, specifically negative pressure, was needed. He readily found data for wood and took it as a comparative standard. Using data for six different species of green pine from a mechanical engineering handbook, he took the average strain at elastic limit, 0.32%.²¹ The data were typical for softwood in a green state and differ modestly from properties of other types and conditions of harvested wood.²² The 4.7% value for *Kalmia* was fifteen times greater, suggesting to Briggs that stretched fibers of the filament did indeed require the additional effect of negative pressure. Surprisingly, nothing in the archived materials suggests that Briggs or Frankland calculated Young's modulus for the filament material, even though they had measurements for the quantities necessary to do so. Specifically, the ratio of their extreme fiber stress to extreme fiber strain gives a value of 2.5 megapascal. This value is comparable to the 1–10 megapascal range that Gardner and Ehlig measured for leaves of four species, perpendicular to the plane of the leaf.²³

In undated notes written after Briggs's experiments of May–June 1956 and before his partial manuscript of May 1958, Frankland stated:

It is plausible that the tubular section of the stamen flattens during the bending and that this reduces the ranges of strain actually experienced by the extreme fibers. Should this happen, then a compressible fluid inside the stamen can do work, since the flattening of the section is accompanied by a reduction in volume. For positive work to be done, it must be at less than atmospheric pressure.

Motivated by the hypothesis that the calculated elongation of the extreme fiber is unreasonably large for a botanical tissue, Frankland is suggesting the actual strain may be reduced by contraction of what he calls the tubular section of the stamen.* Negative pressure of the liquid within the stamen would aid in this process. Plant physiological processes, for example evaporation through pores or alteration of the restriction controlling liquid flow into the stamen, could vary the pressure. Because pressure represents energy density, these processes could increase the energy available to do work in flinging pollen.

Earlier, on October 15, 1955, Briggs wrote: "Could the negative pressure be computed from the work done by the stamen in throwing the mass of pollen a measured distance?" The accompanying diagram of an arc of a measured height and width suggests he was considering using a measured trajectory. With additional knowledge of the pollen mass, he could have computed its kinetic energy and equated that to work done by (and hence energy stored within) the filament. He apparently left no record concerning any attempts to measure the mass of the ejected pollen or other quantities needed for this calculation, including other

* Unfortunately, this conception of the stamen having a circular cross section and a hollow chamber along its axis does not correspond well with the actual stamen anatomy, as described below.

assumptions that would have been necessary to infer the negative pressure once the work was known (such as the unknown portion of the stored energy that would go to dissipative losses). Clearly, however, Briggs and Frankland were thinking that because the calculated material properties seemed unreasonable without some additional mechanism taking up some of the apparent extreme fiber strain, internal fluid at negative pressure could provide that mechanism.

Briggs's 1958 manuscript begins with a description of the flower's anatomy and its unique pollen-release mechanism. The next section is headed "Curvature not attributable to fiber strain" and derives from Frankland's analysis and Briggs's comparison to wood properties. There is no mention here or elsewhere in the archived materials of an estimate of the required value of negative pressure.

Follow-Up Investigations

In order to reconsider Briggs's theory, we studied *Kalmia* stamens that had been collected for one of the authors' (Hermann's) PhD dissertation on stamen development of Ericaceae.²⁴ We photographed and measured filament cross and longitudinal sections using material from both cultivated and wild plants.²⁵ As can be seen from the images in figure 5, the filament is fairly flat, like a ribbon, with the wide faces in the adaxial and abaxial directions. The basal end of filament tends to be slightly concave toward the adaxial side (figure 5a). This tendency reverses to the other (abaxial) direction in the middle and distal portions of the filament (figure 5b). Close to the distal end, the filament becomes more triangular in cross section, with the wide base toward the abaxial side. The adaxial/abaxial flattening of the cross section may be mechanically important in the flinging of pollen, perhaps to maintain a directionality of the stamen's motion that maximizes the upward and outward dispersal of pollen.

Cells are noticeably larger on the abaxial side at the basal end (figure 5a), which may be related to the generation of stress essential to the flinging motion of *Kalmia* filaments. Figure 3 shows the filaments curving outwards to get the anthers inside the corolla pockets. The only way they can do this is by elongation of the adaxial epidermal (and neighboring) cells. Therefore at this level, the adaxial epidermal cells might get longer than the abaxial ones. The size and shape of the cross sections differ from the hypothetical geometry used by Frankland in his calculations, as diagrammed in figure 6.

The botanical structure that, in a sense, constitutes a chamber filled with liquid at negative pressure is the vascular bundle (figure 5), the main conduit for liquid and nutrients in longitudinal transport through the plant. In the middle of the filament, the vascular bundle is close to the center of the cross section (figure 5b). Near the basal end, however, this bundle is considerably off-center in the adaxial direction (figure 5a), so that compressive stress resulting from negative pressure within it would increase the pollen-flinging force when the stamen is released from its pocket.

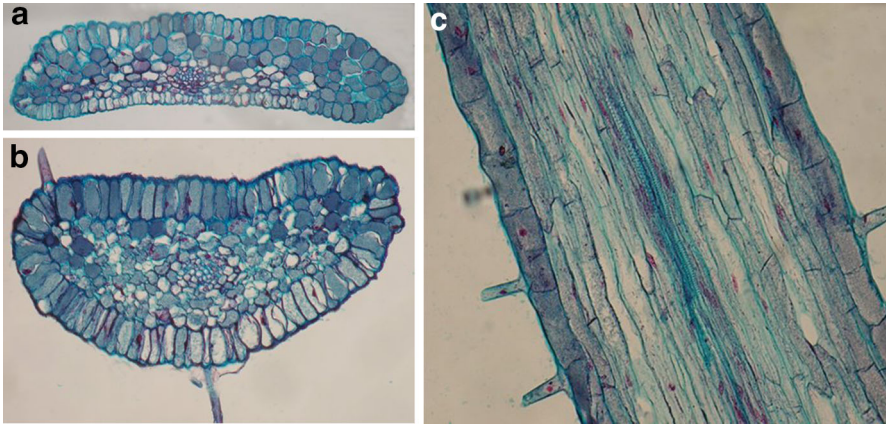


Fig. 5. Cross and longitudinal sections of *Kalmia* filament. **a** Cross section near the basal end of the filament; the vascular bundle is the cluster of small cells approximately centered laterally and offset toward the adaxial side. **b** Mid-filament cross section with vascular bundle at the center of the section. **c** Longitudinal section. Orientation: abaxial side toward the top in **a** and **b**; abaxial side to the left in **c**.

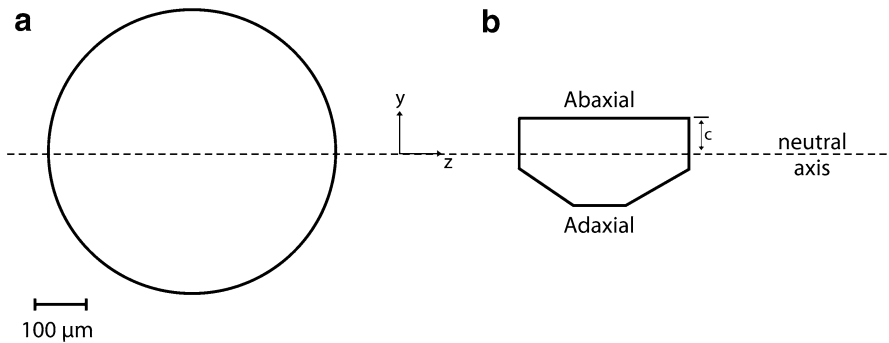


Fig. 6. Idealized cross-sectional geometry of a *Kalmia* filament. **a** Circular form used by Frankland to calculate extreme-fiber stress. **b** Combined rectangle and trapezoid approximating the image in figure 5b above. Both images are to the same scale.

Our field observations show the distance traveled by pollen propelled by the flinging motion range from 2 to 15, typically about 4 to 12 cm. After release, curling of the stamen continues, consistently in the adaxial direction.²⁶ This curling can go as far as about 270 degrees, as was also noted by Briggs. Adaxial curling continues for about 90 minutes, after which time the tight curl begins to relax. Stamens triggered by dissecting probe or by stimulated heavy rain become recumbent or flat, typically within 6 hours, though sometimes taking as much as 24 hours. Up to a day after flinging, stamens divide into four categories, with

varying degrees of relaxation from the tight inward curl: (1) still curled inward; (2) axially erect; (3) recumbent (distal end of abaxially-extended filament and its anther in a slight, C-shaped inward curve, like a person beginning to do a sit-up, with anther raised above corolla bottom); and (4) fully extended abaxially and flat, with filament and anther laying against base of the corolla and the anther laying near its original pocket opening. At least for cut flowers, after flinging the stamens first assume a tight adaxial curl, then slowly uncurl to an extended position, with the discharged anther lying atop the pocket opening.

An issue bearing on the hypothesized role of negative pressure in the *Kalmia* filament is whether wetness of the flower has the effect of suppressing the flinging response of the stamens. The issue arises in Briggs's notes, in an entry that is undated though clearly written a few days after Briggs conducted successful measurements on May 31, 1956:

Practically all open flowers inoperative following rain night of [Friday] June 1 and all day Sat. Stamen flat. No spring.

If ambient moisture did have this sort of suppressing effect, it could be construed as evidence supporting Briggs's concept of negative pressure underlying the flinging behavior because surrounding moisture might decrease the magnitude of this pressure. This behavior could be beneficial for propagation of *Kalmia* because in rainy weather the pollen grains do not disperse as effectively and bee activity is reduced. In our observations, however, the strength of the flinging mechanism was not significantly affected by exposure of the flower to water by spraying, immersion (up to 1 hour), natural rain, or simulated heavy rain.

The other side of this issue is whether unusual dryness affects the flinging motion. On this, some evidence comes from experiments on cut flowers, removed from the stem that supplies internal moisture. Cut flowers that have been in wet storage 36 hours after cutting, if not shriveled, can still undergo rapid, manually triggered flinging. This is consistent with Briggs's observation that flinging is unimpaired by cutting at the stem and removing the flower from the rest of the plant.

On the whole, the available evidence on the effect of flower wetness does not rule out an essential role of negative pressure in flinging, nor does it significantly support this hypothesis. Assessment of the issue of basic filament materials on their own being adequate to cause the observed flinging behavior requires further exploration, detailed elsewhere.* Also important to consider is that component materials within a botanical member differ widely in elastic properties. Data suggest that parenchyma (internal material within a root or stem) is less elastic (has much smaller Young's moduli) than other component materials. Assuming that materials like these dominate elastic behavior of the *Kalmia* filament, in contrast to stiffer sorts of materials likely dominant in wood, this filament's

* Additional details are available at http://www.rcamnl.wr.usgs.gov/uzf/abs_pubs/papers/Nimmo_et_al.2014.Pollen_Dispersal_Biomechanics.appendix.pdf.

properties overall do not seem unusual. This conclusion conflicts with Briggs's concept of an elastically-aberrant quality of the filament. Critiquing his unpublished work in hindsight, we are drawn in a different direction through having a more accurate description of the filament anatomy and a wider range of botanical materials to compare with.

Indeed, seemingly minor discrepancies between the actual geometry of a *Kalmia* filament and the geometry assumed by Briggs and Frankland could support the wrong conclusions about the pollen-flinging mechanism. Briggs's overemphasis on the need for stress augmentation shows that, while rigorous physical analysis has much to contribute to the understanding of botanical tissues and processes, a precise knowledge of the botanical structural elements is essential.

During development from bud to mature flower, stamens go through a rapid elongation phase. Bending stress could be generated either by a faster growth rate of the filament than the corolla or by a differential elongation within the filament that would be faster on the abaxial than the adaxial side. Kress notes that

there were only two main interpretations when I wrote my Phytologia paper: [Stress] grows with filament length (European scientists)—and [stress] of filaments is caused by becoming bent back in growing buds and opening flowers (American ones). Whether the outer side of the filaments is growing faster than the inner one or the turgor increases more in the former than in the latter, or both, remains undecided.²⁷

Turgor refers to the hydrostatic pressure exerted on cell walls that contributes rigidity to the plant's structure. As a positive pressure in the material surrounding the vascular bundle, turgor provides a complementary way of conceptualizing axial pressure differences within the filament. Kress additionally observed evidence from an increase in the possible degree of filament motion as the flower develops, so that

in newly opened flowers the angle of bend will often not even reach 90°, while 270° will sometimes be exceeded in older (though not spent) flowers.²⁸

Concerning the possible means of creating a bending stress through elongation of the filament during flower development, Hermann and Palser observed that in several genera including *Kalmia*, “the initial relatively slow growth of the filaments is followed by very rapid elongation just prior to anthesis [opening of the flower].”²⁹

The elongation hypothesis for creation of bending stress raises further questions. Is the magnitude of stress generated by elongation on its own enough to cause the observed flinging behavior? How is it affected by wetness of the flower? Do pressures internal to the stamen (implied by Kress with his mention of turgor) supplement or dominate whatever stresses result from elongation? Consideration of Brigg's hypothesized role of negative pressure provides further illumination of these issues.

Though negative pressure is not essential to give the *Kalmia* filament the observed elastic properties, it may still play an important role, for example in generating bending stress within a member that was formed in place, as opposed to one formed in an unstressed position and then repositioned to create stress (as in a mousetrap). To create a directional bending stress by means of an inherently nondirectional internal pressure, the filament cross section must be asymmetric in stiffness.* If one side of the filament is stiffer through having greater Young's modulus or greater thickness, its hydromechanical character would be analogous to the thermomechanical character of the bimetallic strip in some types of thermometers.

Greater stiffness might result from excess lignification, as is the case within coiling cucumber tendrils (lignin has a high Young's modulus), or possibly from greater thickness of parenchymatic tissue on one side of the vascular bundle.³⁰ The filament cross-sections in figure 5 show considerable variation in shape and other characteristics. Features of note include (1) location of the vascular bundle closer to the adaxial than the abaxial edge (figure 5a), in some cases with the vascular bundle essentially at the adaxial edge; and (2) a somewhat triangular cross section (figure 5b) with two of the three main lobes of parenchymatic tissue on the abaxial side. These suggest greater stiffness on the abaxial side, as would be needed to contribute positively to the bending moment that flings the pollen.

Another advantage of negative pressure to generate stress is that it can be adjusted more quickly because it does not require tissue growth or permanent transformation. Rapid adjustability could afford an advantage in promoting flingability at optimal times for pollination, as discussed above in connection with the effect of flower wetness. Thus, even without the need for negative pressure to create unusual flexure properties, as Briggs hypothesized, we are left with the possibility that negative pressure may play an important role in generating the stress within the filament necessary to cause the forceful flinging of pollen.

Conclusion

For Briggs, his experiments with *Kalmia*, done when he was in his eighties, were a continuation (albeit after a forty-year hiatus) of research begun at the USDA's Bureau of Plant Industry (BPI), where he headed the Physical Laboratory** from 1906 to 1919. A portion of his plant biophysics work was summarized in a presentation entitled "The Living Plant as a Physical System," which he gave to the January 1917 gathering of the Philosophical Society of Washington as its retiring president.³¹ In this address, he highlighted his work on evapotranspiration done

* It may be helpful to note the rigorous definition of stiffness as the ratio of imposed force to resulting displacement of a body, an extensive property based on dimensions as well as an intensive material modulus.

** Later renamed the Biophysical Laboratory.

with botanist Homer L. Shantz (1876–1958), who went on to become the president of the University of Arizona. Briggs and BPI colleagues also worked on the development of microscopy using UV light to examine fine detail in biological specimens.³² In his post–World-War-II return to biophysics, Briggs’s interests focused on negative pressure in plants, with a particular interest in the height of water rise in trees.³³ His *Kalmia* investigations seem to have been a spin-off of that overarching interest.

Briggs was at the forefront of applying physics to complex biological problems in the 1950s, when biophysics was just beginning to emerge as a discipline. The Biophysical Society was founded in 1957 and began publishing the *Biophysical Journal* in 1960.³⁴ This pioneering role was not a unique experience to one who served as presidential science advisor (to F. D. Roosevelt on the consequences of Einstein’s atomic bomb warning) before such a formal position existed.¹² Briggs’s work establishes him as a pioneer in biophysics and interdisciplinary science. Examination of 1950s era plant physiology textbooks suggests that Briggs introduced a level of physical science expertise and thinking not typically seen during this period.³⁵ Drawing on his talent pool at NBS, he was able to bring in structural-mechanics expertise not found in biological science research groups.

Nearly six decades after Briggs took on this problem, current knowledge still contains gaps that leave room for doubt about the answer. The problem and its incomplete resolution highlight the fact that important questions of pollen dispersal mechanisms and internal plant-water relations require expansion of our understanding of biophysical properties and the dynamic behavior of plant tissues.

Acknowledgments

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[Figures are in the published paper.]

Biomechanics of pollen-flinging

Briggs's (1954-1958) analysis was the first attempt to apply rigorous physical theory to the pollen-flinging mechanism of the *Kalmia* flower. More recently, Niklas (1992) has given a physical description of the flinging biomechanics of a related species, *Kalmia angustifolia*. Here we present some of the physical reasoning and calculations apparent from the materials Briggs left behind, with updated interpretations made possible with recent knowledge of the filament geometry and the properties of related botanical materials

The bending of the filament of the *Kalmia* flower is an inherently two-dimensional problem involving curvature and transverse forces. Desirable simplifications result from transforming it into a largely one-dimensional problem of simple lengths and displacements. Briggs and Frankland did this by the standard method of extreme-fiber analysis. The filament is conceptualized as a tight bundle of infinitesimally thin hypothetical fibers. Here the word "fiber" refers to a hypothetical geometric element, and does not correspond to any physical botanical structure. Each fiber experiences a particular longitudinal stress and strain caused by the bending stress. Fibers at the edges that experience the greatest stress are called the extreme fibers; in the *Kalmia* filament these are at the extreme ad- and abaxial positions. Briggs' measured dimensions indicate extreme fiber strain of 4.7% for a filament bending through 270° as in figure 4.

Frankland calculated extreme fiber stress using the flexure equation, which defines bending stress as

$$(1) \quad \sigma_x(y) = \frac{My}{\int_A y^2 dA},$$

where M is the bending moment (the product of length and applied force of the filament, considered as a cantilever beam loaded at its distal end). Briggs's measurements give a bending moment of 2.0 μNm ; A is the area of the beam's cross-section. The coordinate x is in the longitudinal direction of the beam, and the y - z plane is normal to it (figure 6). The coordinate y is in the direction of the bending force and has its origin on the neutral axis, defined as the set of points in the y - z plane at which the bending stress $\sigma_x(y)$ is zero. Conceptually the neutral axis is the line that stays fixed when the beam is bent, around which the off-axis portions of the beam tend to rotate. The integral in the denominator is frequently called the moment of inertia, though because it includes no inertial mass, it is less confusingly called the second moment of the cross-sectional area.

With limited knowledge of its actual physical characteristics, Frankland conceptualized the filament as tube of circular cross section filled with fluid (in some instances referred to a gas). He assumed the material was homogeneous, so the neutral axis was simply a diameter. Given an outside radius R , the extreme fiber stress is $\sigma_x(R)$. He calculated stress for various tube wall thicknesses. An actual filament internally comprises cells and intercellular spaces without a singular chamber resembling the interior of a tube, and it does not contain significant gas. Thus, the most relevant of Frankland's calculations is the one having tube wall thickness equal to the tube radius, i.e. a rod rather than a tube. The area of integration A being a circle, with Briggs' data and Frankland's assumed geometry, the calculated extreme fiber stress is 0.12 MPa.

Frankland, though he appropriately used the mid-filament thickness 250 μm when he was calculating extreme fiber strain, took the diameter of the circular cross section he used for calculating extreme fiber stress to be the basal lateral thickness of the filament, 560 μm . This unrealistically large size is apparent in figure 6. The distribution of stress from a given bending moment over a larger area makes any given fiber stress less; this large area in the integral in (1) leads to Frankland's value of extreme fiber stress. The small value he obtained was unrealistic for a beam whose own unaugmented stress could accomplish the *Kalmia's* flinging of pollen and thus contributed unwarranted support for the argued necessity of negative pressure contributing a major component of the stress.

Unlike the circular geometry, whose symmetry locates the neutral axis exactly on a diameter, the more realistic geometry requires a calculation of its position. For this, we assume homogeneity of the filament material, which is not strictly true (from figure 5 it is clear that the cross section contains different materials, cell sizes, and structures) but may be adequate for evaluating the reasonableness of computed values. Assuming also that the bending is entirely in the elastic range (Hooke's law applies throughout), stress and strain in the bent filament increase linearly with y , whose zero is on the neutral axis. For the static case, appropriate to the pinned filament, compressive stress over the area above the neutral axis must balance the tensile stress over the area below. This condition determines the location of the neutral axis (n.a.):

$$(2) \quad \int_{\text{Area-above-n.a.}} y dA = \int_{\text{Area-below-n.a.}} -y dA$$

In words, the first moment of area must balance across the neutral axis.

Integration over the indicated polygonal shapes with the measured dimensions gives the neutral axis position as 74 μm from the abaxial edge. Integrating with the second moment of area in the flexure formula (1) gives the bending stress $\sigma_x(y)$. Using Briggs' measured bending moment M , the abaxial ($y = c$) extreme fiber stress is 1.45 MPa. Recalculating the extreme fiber strain (again for the filament going through the 270° bend shown in figure 4), using our estimates of the filament dimensions we obtain a value of 0.036, smaller than Frankland's 0.047 because of the smaller filament thickness. The ratio of stress to strain then indicates a Young's modulus of 40 MPa, larger by a factor 16 than what Briggs and Frankland's analysis would have given (Table I). This larger value indicates greater ability of the filament to apply force from unbending, and so diminishes the need for Briggs' hypothesized augmentation of the force with negative pressure.

The second area where new knowledge can enhance Briggs's interpretation is in the properties of relevant materials. Elastic limits of botanical materials are rarely measured outside of construction applications; most such measurements are for wood used as a construction material. In Table I we have compiled measured and computed values of such properties for the *Kalmia* filament and other materials selected for comparison. Young's modulus is the one property known for all items here.

TABLE I. Elastic properties of selected materials of botanical origin.

Material	Extreme Fiber Strain	Extreme Fiber Stress (MPa)	Young's Modulus (MPa)	Strain at Elastic Limit	Stress at Elastic Limit (MPa)
<i>K. latifolia</i> filament-- Briggs/Frankland values (Briggs, 1954-1958)	0.047	0.12	2.5		
<i>K. latifolia</i> filament--our values	0.036	1.45	40		
Pine wood (Marks, 1930)			8030	0.00314	25
Riparian stems and branches (Sutuli and others, 2012)			4540	0.015	45
Parenchyma (Niklas, 1992)			50		
Lignin (Cousins and others, 1975)			3300	0.067	220
Cellulose (Niklas, 1992)			400000		
Parenchyma of <i>Pachycereus pringlei</i> (Niklas and others, 1999)			4.6 to 9.6		
Stem rib tissue of <i>Pachycereus pringlei</i> (Niklas and others, 1999)			1900 to 2800		

The measurements of Sutuli and others (2012) for stems and branches of four species of riparian plants are more appropriate for comparison than the wood (lumber) data available to Briggs. The motivation for these measurements was not to assess suitability for construction but rather to understand the performance of streambank vegetation in altering flow patterns within the river and reducing erosion. The stems and branches measured are relatively young and thin, so perhaps more similar to a *Kalmia* filament. Compared to wood used for construction, these have a smaller Young's modulus, greater capacity for stress in the elastic range, and much greater strain at elastic limit (1.1% to 1.5%). On the whole these properties suggest much closer resemblance to a *Kalmia* filament.

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